EUGENE MUNROE

Biosystematics and

Dynamic Ecology

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EUGENE MUNROE *Biosystematics and Dynamic Ecology*

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The Process of Classification

Classification is a task that confronts us daily, in a wide variety of activities, scientific and non-scientific. It is so familiar to us that we often find it hard to think critically about either the problems involved in classification or the reasons for trying to classify. As the reasons give the key to the nature of the process, we must consider them first.

The primary and simplest object of classification is to be able to relocate a particular element at will. A classification of this sort may be completely arbitrary, with its only order that introduced by identity numbers or geographic positions. Examples are assignments of miscellaneous objects to a set of pigeonholes or serial numbering of a set of specimens by order of collection or preparation. Such classifications are of great practical value, as shown by telephone directories, automobile licensing systems, and the like.

Certain principles apply in the design even of a purely arbitrary system of this kind. The system should permit simple filing and extraction of information, and the configuration of the system should be functionally related to the physical application of its contents — telephone directories are published by cities and their numbers are coded by exchanges; the contents of bureau drawers are arranged by their expected use. Confusion of items should be excluded or minimized. Often features that facilitate remembering of item or category labels are an advantage.

Often it is not sufficient merely to relocate individual items at will. We may require to group similar items in categories and even to group categories in a hierarchy of varying complexity. Biological classifications are usually of this nature. New problems are inherent in this type of classification. Among these are the definition of categories, the unequivocal assignment of items to them, and the arrangement of categories in an advantageous system. Philosophical complexities, surprising to the layman or to the unwary scientist, underlie these problems. However, I shall skirt such questions and discuss briefly only how the problem of ordered classification presents itself to the working biologist. The dimensions of this problem are determined in part by general principles and in part by the nature of the materials to be classified and the use to be made of the classification. The principles are relatively simple and I will discuss them first.

Individuals can be assigned to groups in different ways. Some single defining character or combination of characters can be used. A simple classification may permit a *yes* or *no* decision on inclusion on the basis of such a character or combination. More sophisticated classifications may have to provide for such categories as *maybe, intermediate* or *sometimes.* Combinations of defining characters of the *either-or* type present greater difficulties of recognition. A third use of character depends on their probability distribution rather than on their presence or absence; this applies particularly in the overlapping probability distributions of quantitative characters or where assignment is based on preponderance of a number of individually variable yes-or-no characters.

A second different way of assigning individuals to groups is by subjective or objective judgment of their resemblance to types or norms, which may be either real individuals or conceptual composites. In the latter event our concept may be either that of an "average" individual or that of a generalized individual taking into account the essential and variable characteristics ascribed to the group. This method attains its greatest success in classifying entities that fall into rather sharply separated categories. It tends to fail where there are many intermediates between different norms. Such failure can often be avoided by increasing or decreasing the number of norms, with corresponding modification of the accepted range of variation. In practice much biological classification is based on such procedure, which, if used with an understanding of their limitations, form a valuable taxonomic tool, and one that is readily supplemented or replaced by methods based on explicit characterization in areas where it shows weakness or confusion.

A third way of assigning individuals depends not on their similarities and differences but on their functional relationships to one another. Such a basis implies an experimental approach and a knowledge of the dynamics of the assembly to be classified. If valid correspondences can be established between classifications based on similarity and those based on functional relationship then the one can be used interchangeably with or to supplement and add to the other. A correspondence of this kind is that between chemical properties and atomic structure expressed in the periodic table of the chemical elements.

The classification of groups of individuals, as opposed to the assignment of individuals to groups, presents some of the same problems and some different ones. It may be possible to assign all individuals of an assembly unequivocally to well-defined primary groups and yet to have several different ways of classifying the groups and determining their degree of similarity, depending on the criteria used. If, as in biological classification, we wish to erect a hierarchical array of groups of different ranks, then problems arise of the number of ranks and the equivalence of ranks in different sequences of subgroups.

The Materials to be Classified

We could analyze the process of classification much more thoroughly than I have done here, but we cannot intelligently decide what kind of classification to adopt until we survey some of the characteristics of the units we propose to classify, and until we have some idea of how we want to use our classification.

Living things may be thought of as the physical manifestation of complex processes, involving continuing changes in both the living components and the non-living, environmental components of the ecosystem. It is customary to base the primary biological classification on the living components only. This practice is justified by common experience, which tells us that the living components are to a large extent divided into repetitive and very frequently discrete systems which we call *individuals*, and that these individuals can to a considerable extent be classified into more

or less obvious kinds or *species*, with essentially definite and predictable characteristics, both of structure and of action, which in general have not changed materially over the span of human observation. So obvious is this separability into species that in almost all societies, primitive or civilized, including our own up to the last century, the species have been accepted naively as part of the fixed order of the universe. Accounts of their formation are typically found in creation stories. It is only the exceptional curiosity of Western man concerning his environment and origins, his unprecedented store of factual information, and the power of his scientific methodology and tradition that have led him to a different view.

On closer examination we find a number of things that alter our concept of these supposedly natural species. The first and most evident is that the individuals are mortal and mutable. Not only do they die or divide, to be replaced by offspring of themselves or their contemporaries, but they go through a repetitive cycle of greater or less length from birth to death or fission. The aspect and properties of the individual may vary greatly from one part of the cycle to another. Indeed, whole generations may be involved in the cycle, the parent type being repeated only after two, three or more episodes of reproduction. The relationship between an insect larva and its adult, say, is purely a functional one, not evidenced in any morphological character above the cellular level. Only by taking a composite space-time view of the individual, or even of a sequence of several generations, can we achieve a one-to-one correspondence with another individual taken at a different life-stage, and such a view is rarely the result of direct observation.

A second problem is that two individuals, even at the same life-stage, are rarely if ever exact duplicates. It is well known that the individual is the product of heredity and environment. On the one hand the vast array of potentially different alleles makes it mathematically highly improbable that two individuals should ever share exactly the same hereditary constitution. Even if this were to occur, it is even more unlikely that the two would encounter environments similar enough to prevent the development of some environmentally determined differences in a lifetime. It is true that selectively determined homoeostatic mechanisms tend to lessen the apparent differences between genetically diverse individuals within a species, but this levelling is an approximate one only, and in its turn subject to the modifying effect of the variable environment.

A third problem is that introduced by sex. Morphological differences between sexes are often striking; differences in behaviour are usually profound. The identification of sexes of a species, like that of life-stages, often depends on a functional relationship—either the observation of mating, or, more certainly, the rearing of both sexes from the progeny of a single mother. This functional criterion introduces a whole new concept of the species—what Dobzhansky called the dynamic species concept, that is the definition of the species as a mating system. The essence of Dobzhansky's concept was that if two populations, not prevented by extrinsic physical barriers from freely interbreeding, maintain their separate identities over an indefinite number of generations, they belong to separate species. In Dobzhansky's view, the morphological and functional similarities that unite

individuals of the same species and divide them from individuals of other species are the secondary consequence of the presence or absence of interbreeding. On the average, distinct species can be expected to differ markedly because of accumulated genetic differences, but we must expect a proportion of atypical or *sibling* species pairs or sets in which the phenotypic differences are small because of recent separation or slow genetic divergence. Apomictic populations do not fall readily into this scheme, for there is no cohesive process comparable to the recombination of genes in outbreeding populations to bind their clones together. They do not form species in the Dobzhanskian sense, though for convenience of reference they may be divided into taxonomic species based on degree of morphological or other difference.

In considering either static or dynamic criteria of classification, we must take into account one further factor: the slow *evolutionary* change of populations and systems of populations over the course of geological time. This change, now almost universally accepted as a fact, has several implications for classification. One of the more important is the difficulty of defining species in time, as they change by slow accumulation of genetic differences from generation to generation. This implies a corollary difficulty in distinguishing contemporaneous populations that are incipient or newly separated species at the critical stages of their divergence. Evolution both at the specific level and at the levels of the various higher groups has obvious importance as the process generating the arrays of forms and differences that provide the subjects and criteria for our classification. Acceptance of the principle of evolution has made it possible to make a classification of relationships running closely parallel to the classification of similarities provided by the study of morphological and other observed characteristics. Though there is still dispute over which of these classifications ought to be ranked as the primary one, there is no dispute as to their close general correspondence or as to the importance of each in shedding light on the other.

THE ARRAY OF BIOSYSTEMATIC MATERIALS

Importance and Biosystematics for Ecology

I have elsewhere (Munroe, 1958) discussed the practical importance of the identification process as an adjunct to ecological research. What I wish to emphasize here is the close relationship of the statistical, dynamic, and geographic aspects of systematics on the one hand and ecology on the other. Dynamic ecology is the study of the functional interrelationships of biological species with one another and with the inanimate environment. Systematics is to a large extent the study of the nature and distribution of the components entering into these relationships, and of the genesis and results of the relationships, considered as long-term processes.

Structure of Species

For the present purpose we must consider species from the dynamic aspect, that is, as assemblages of individuals linked by common properties of

reaction to the environment, and by reproductive linkage close enough to exclude wide genetic divergence. This linkage may be vertical, i.e., through common ancestors, but in outbreeding organisms it is horizontal also, through conjugation or sexual union. The Dobzhanskian and non-Dobzhanskian species are both encompassed by this definition, but the reader will realize that the former can be defined with some degree of precision in dynamic terms whereas the latter is purely a division of convenience.

The functional structure of species can be studied from many different aspects, several of which are important to dynamic ecology. The first is the distribution of the biomass among individuals. Whether the individuals are large and few or small and numerous represents a fundamental difference in the "strategy" of the species. Large individuals can carry heavier insulation and armour, stronger weapons, more powerful tools, and more complicated sensory and co-ordinating equipment. The probability of individual survival can therefore be increased and stabilized, up to a point. Against this have to be balanced at least four types of factors. The first of these is increase in the volume/surface, volume/cross-section and volume/length ratios, giving rise to difficulties in chemical and thermal interchange, in support and motion, and in leverage, co-ordination and internal transport. The second is loss of flexibility in coping with changes in resources. Large organisms need large ranges and large food supplies. A local diminution that small individuals could cope with by reduction of the population might be fatal to even a single large individual. The third is the statistical danger of putting two many eggs in too few baskets. A small population of individuals of relatively high individual survival potential may be more open to the danger of extinction through the accident of nearly simultaneous death than a large population of relatively much lower survival capacity. The fourth danger is genetic: numerically small populations are more exposed to the deterioration of genotype caused by random fixation of non-adaptive alleles; also, large individuals commonly have long generation times and correspondingly slow evolutionary rates, resulting in relatively slow adaptive response. Not only is the distribution of biomass of mature individuals important, but also its distribution through the life cycle. Offspring may, for example, be few, large, and of high survival potential, as in most mammals, or small, numerous and subject to high mortality, as in many invertebrates. With similar numbers and sizes of offspring, mortality may be high early in life, or may take place mainly at later stages, after considerable growth has taken place. In the former case the tax on food resources is much less than in the latter, though the end result from the standpoint of the population of mature individuals is the same.

A second important feature of the structure of populations is the distribution of individuals. Distribution is important in many ways. A restricted range carries with it a relatively higher danger of extinction because of the possibility of adverse change in the local environment. A wide range, as has been shown experimentally for many species, is associated with differential adaptation to varied local climates and environments. Distance affects the possibility of reproduction, so that population density rather than population number describes and governs the local progress of the species.

However, occurrence over an extensive range means that there are normally reservoirs in adjacent areas tending to level off unusual swings in local population density whether intrinsically or extrinsically generated. The pattern as well as the extent of distribution is important. Aggregation may confer some of the benefits of dense population without unduly taxing the resources of the environment. Overdispersion may permit more effective or more even exploitation of resources than would be possible with a random distribution of individuals.

A third main aspect of species structure is the distribution of genetic material. This is functionally related to the distribution of individuals, but, as is well known, genes can exist in individuals in sets of two or more, which are not necessarily identical and of which one may be dominant over the other in determining the characteristics of the developing individual. In sexually reproducing organisms the genes segregate in the gametes and are recombined in the zygotes of the new generation. If mating is free and random, the recombination is also random, except for physical linkage of genes on the same chromosome. Selective mating, fertilization, or survival of zygotes on the one hand or obstacles to free interbreeding on the other generate non-random patterns of recombination. Recombination has a levelling effect from generation to generation on a population that forms a freely interbreeding system. Populations that do not interbreed freely, on the other hand, tend to diverge in their characteristics, partly because of the accumulation of random differences in gene frequencies and partly because of differential selection if their environments differ.

A complex, though still far from mature, science of population genetics deal with these phenomena. I may mention some of its simpler conclusions that are of interest to us. In recombination from generation to generation the expected value of the gene frequency remains constant, though stochastic variations occur more appreciably in small populations. Selection, mutation, or introduction of extraneous genes at determined rates change gene frequencies in a progression that is predictable in terms of expected values, or that has a predictable probability distribution, considered stochastically. The achievement of individual genotypes is determined by the matrix of probabilities of simultaneous combination of the different alleles present, given the relative frequences of alleles present and the relative viabilities of the zygotes represented by each of the possible combinations of alleles. Obviously such a calculation is impossible in practice except for a few selected genes and alleles that may interest us particularly. Obviously also, even in a very large population the possibility of any particular total genotype being represented is very minute. As both mutation and selection rates are affected, sometimes strongly, by total genotype, it is only a first approximation to treat these as definite quantities in the equations of population dynamics.

Certain features of the gene pool have special interest for population ecology. Among these are the existence of a rather constant phenotypic "wild type" in many organisms, maintained by dominant alleles, and the co-existence of a large pool of deviant recessive alleles, a proportion of which are expressed phenotypically by recombination in each generation.

It has often been noted that this arrangement permits close adaptation to normal environmental conditions but holds considerable variability in reserve to meet abnormal conditions should they arise. Another characteristic of the gene pool that we may note is the existence of various arrangements that maintain polymorphism in a balanced state in the population. The balance may be a static one, such as that induced by lethality of homozygotes in various lepidopterous colour-forms, where diversity confers a selective advantage on the population, or it may be a swinging balance, either seasonally controlled, perhaps having adaptive value for survival in a variable climate, or density controlled, perhaps taking part in the actual arrangements for control of density in populations.

Geographical barriers, whether or not coupled with ecological differences, may result in the fragmentation of Dobzhanskian species into populations that are partly or wholly isolated reproductively because of the limitation or absence of contact between their individuals, and that differ appreciably in their gene pools. These populations form the first step in one kind of speciation and are called subspecies. Different subspecies may be adapted to very different ecological roles. Geographic chains of subspecies are known with overlapping ends, the end members being different enough to act towards each other as distinct, sympatric species.

Structure of Higher Taxa

Once the level of the interbreeding, Dobzhanskian species is passed, we are faced with a new situation. There is no longer the conservative force of recombination to impede divergence within the assemblage, and more than one population of the group can exist in one place at the same time. By extinction of species, gaps can be left in the array of variation, and we usually find a set of larger or smaller clusters of species of greater or less similarity. These form the basis for genera and other higher taxonomic groups.

The fact that we arrange species in such groups indicates that they have considerable similarity. This similarity may extend to their way of life. Almost all swallowtail butterflies of a certain group, for example, feed on plants of the genus *Aristolochia*. Where their geographic ranges of such species overlap, they are more likely to compete than species chosen at random. There are indications that species often tend to eliminate or affect adversely their close relatives in zones of overlap. Sometimes we observe what is called *character displacement* (Brown and Wilson, 1956) in such zones, that is, the characters of one or both species are changed in such a way as to decrease the similarity between them. Such displacement may arise because of selective tendencies of two kinds, one tending to decrease the probability of nonproductive or disadaptive interspecific matings, the other tending to decrease ecological interference of the species in the zone where they have a common habitat.

There is considerable difference among higher taxa in numbers, variety, and continuity of range of variation of their species. Some groups are small and show little diversity. These may be the last successful remnants of formerly more extensive lines, as in the elephants or camels, or they may

be groups like the crocodiles which have found a moderately successful plan of organization and which have not departed from it. Other groups though small may show great diversity. These are usually relicts of more extensive groups. From the ecological standpoint large groups are often more important. These may be diverse, like the mammals. Like that group they may preserve a reasonably continuous range of variation (though we know that many mammal groups and species have been lost with time) or, like the reptiles, they may have very wide taxonomic gaps separating groups as individual as, say, the snakes or the turtles. Still other groups may be both large and compact, with large arrays of very similar species and genera. Such groups are exemplified by the muscoid Diptera, by the ground beetles or by the passerine birds. Evidently the key to such differences is to be found in ecological success. Some groups have attained highly successful ways of life that have permitted them to invade a wide variety of habitats with a single plan of organization; others have specialized extensively and thus have occupied many habitats but in diverse forms; still others have been cast down from their former high estate and are represented only by isolated survivors. Dr. K. E. F. Watt has pointed out to me the likelihood that such differences in taxonomic structure may be correlated with differences in ecological stability, or other population characteristics. By comparative study of abundance trends in groups represented in the Forest Insect Survey of the Department of Forestry of Canada he hopes to find indications of such relationships.

Canonical Distribution of Taxa

One of the surprising features of the overall pattern of life is that its species, numerous and diverse as they are, are distributed with great statistical regularity. In a series of papers (Fisher, Corbet and Williams, 1943; Williams 1944, 1947), C. B. Williams and his associates showed that in random samples of biotas the number of species represented by given numbers of individuals or observations fell into a series closely approximating to a logarithmic series, in which the largest category is that of species represented by one individual and in which there are progressively fewer species with larger numbers of individuals. The distribution is determined by an index of diversity, which depends on the total number of species in the biota being sampled. If two samples from the same biota are pooled, the pooled sample has an unchanged index of diversity; if the samples are drawn from different biotas, the index is increased.

Preston (1948, 1962) has more recently studied much larger samples, and has concluded that Williams' series is only a first approximation and that the distribution of abundance of taxa is actually log-normal. With large samples the modal abundance is above 1 and the normal curve is revealed to an increasing degree, its lower tail, however, always being cut off by a "veil line", where the expected number of individuals falls below 1. Preliminary studies by Hairston (1959) and MacArthur (1960) suggest that the lognormal distribution may break down when biotas are analyzed to the level of small and uniform habitats, and that it may depend on a proportion of casual mixing of individuals from different habitats. In

any event the regularities shown even by tentative exploration indicate that study of the relative abundances of species is a very powerful tool for the investigation of overall regularities in the ecological process.

Geographical Distribution of Taxa

It is well known that taxa are very unevenly distributed over the earth. Marine, freshwater and terrestrial organisms are different, and there are wide differences according to differing habitat in each of these main spheres of environment. In general tropical biotas are richer than polar ones (the rule is reversed in some marine habitats), moist terrestrial environments are richer than dry ones, shallow marine environments than deep ones. There are many gradations of such regularities. Geographically separated regions tend to have biotas that are ecologically parallel but taxonomically different. Rain-forest or desert biotas in the different tropical continents show great similarity of life form but tend to be composed of different species, genera, families or orders, which often have assumed their parallel adaptations independently. The differences between biotas are a measure of the effectiveness and, in part, of the past duration, of their separation.

The regularities of sample size mentioned above extend also to the natural samples provided by geographic areas (Arrhenius, 1921; Williams, 1947; Munroe, 1953). The biotas of larger areas are richer, following laws closely analogous to those for samples taken artificially. Separate biotas, taken together, have larger indices of diversity as well as greater numbers of species, than single ones. Fragmentation, whether by geography or by ecological difference, into semi-isolated habitats therefore makes for richness of biota. Other factors also come into play. Remote habitats, such as oceanic islands, have relatively poor biotas, in which the descendants of a small number of immigrant stocks are noticed. Some of these may expand disproportionately (as in the Galapagos finches or the Hawaiian honeycreepers), but the aggregate expansion does not compare with that of richer, continentally based biotas. Islands near to continents have richer biotas, with more immigrant stocks. Continents have the richest biotas. All these regularities are of course subject to the regularities mentioned above that are imposed by climate, by habitat type and by degree of fragmentation.

PARTITION OF ECOSYSTEMS

Local System

All local ecosystems depend on availability of living space, on a continuing supply of materials and energy, and on the absence of physical or chemical conditions that would interfere with life processes.

The "fitness of the environment" has been discussed extensively, and I will not dwell on it here. Space in itself is less commonly a limiting factor than the limits on supplies of energy and materials imposed by space. Energy is for the most part of solar origin. Ecosystems depend in general on photosynthesizing plants which trap a proportion of the solar energy and store it as energy of chemical combination. These plants often compete

11

actively for light, as is seen in forests or even in continuous non-arboreal cover. Often the light is filtered out at several layers by plants adapted to operate at different intensity levels. Energy may easily be so abundant that materials are the constraining factor. Water, for example, is needed to support vegetation, especially dense and high vegetation in areas of intense solar radiation. For this reason there are often savannahs or deserts in areas where energy supply would be enough to support a luxuriant ecosystem. Water, as is well known, depends on a rather rapid geophysical circulation, driven by solar energy. Other elements necessary for life, e.g., nitrogen, carbon, phosphorus, depend on geophysical or geochemical cycles, whose rate may impose a limit. In general Liebig's law applies: that factor which is in shortest supply in relation to requirements determines the extent of the whole process.

Energy and materials determine not only the richness of the local system at any one time, i.e., the standing crop, but also the rate of turnover, whether it be measured in terms of metabolic processes or of rate of reproduction and replacement of individuals (generation time). We must not forget, either, the solar energy and sun-driven earth processes are periodic all over the earth, though more strongly so towards the poles. Life processes may be slowed at seasons of low heat supply, or of drought; they may be stopped entirely if temperature or moisture fall below certain critical values.

In any event there is a certain maximum of resources available to any ecosystem at any given time. So rapidly are empty habitats filled up that we can be fairly sure that most ecosystems are operating at close to maximum capacity most of the time. These resources have to be divided among the species present in the system. The rarity of drastic short-term changes in the species composition of natural habitats suggests that some degree of balance exists, no doubt arrived at by selection over long periods of time. The form of division is not arbitrary, but depends as we know, on a complex, interlocking system of food-chains, symbioses and checks and balances. Nonetheless there is a random element in it. Every species is subject to ups and downs and to dangers of depletion or extinction. There is evidence that density-dependent processes and perhaps also close general adaptation to environmental parameters tend to stabilize populations to some degree and thus to reduce the danger of extinction or the closely related danger of over-expansion. However, such protection cannot be absolute. Species must always bear a finite risk of extinction. This risk tends to increase as the number of species sharing a given allowance of resources is increased, as there is then less for each one, on the average each can support a smaller population, and each is exposed to a statistically greater risk of accidental extinction.

As the degree of partition is increased, then, or, to look at it another way, as the richness in species of the biota supported by the same environment increases, the rate of loss of species through extinction tends also to increase, because each species has a greater probability of extinction in unit time and because the mean probability of extinction must be multiplied by the larger number of species. At some level this extinction rate will

strike a balance with processes tending to increase the number of species, namely, immigration of species from outside the local system and autochthonous speciation within it, the latter factor itself increasing as the ecosystem becomes more complex and populous. The level at which this balance is struck is determined by the size of the local system and by its richness in available materials and energy. This combined quantity may be termed *effective living space*.

Systems Extended in Space

If we extend our view from purely local systems to wide geographical areas, then we encounter much more complex patterns and processes. The characteristics of local systems of course form a part of these patterns and processes, but on the broader scene we must consider two important new influences, first the geographical zonation of environments and secondly the effect of distance and difficulty of travel on the interaction of spatially separated ecosystems.

The general fact of geographical zonation has already been referred to, and some of the regularities have been briefly described. It seems likely that gradients in richness of biota from poles to tropics and from deserts to rain forests are determined directly by the parallel gradients in richness in available materials and energy which determine the level of partition at which the system is in balance at any locality. The effective living space per unit of geographic area is higher in places that are richer in available materials and energy, and the number of species is correspondingly high.

Effective living space is determined not only by richness, but also by area, of the habitat. This means that large continuous areas, such as continents, have more species in their biotas than small ones, such as small islands. Up to a certain order of size, characteristic for the type of organism being considered, this increase is strictly related to area. However, in larger continuous habitats, such as large islands or continents, the relationship is modified, and the number of species is greater than we should expect from extrapolation from small islands. This is true whether the number of species in the biota or in some segment of it is measured (Munroe, 1950, 1963) or whether censuses are made of equal areas in the larger and smaller habitat, as was done by Wilson (1959). It seems likely that this break in the species-area relationship is caused by the relatively higher importance of speciation in large areas where both *per saltum* speciation and speciation by geographic differentiation can be expected to take place at higher rates.

The major continents therefore act as centres of evolutionary development—a fact which is well known to palaeontologists and biogeographers. Islands close to the continents derive many immigrant species from them and may contribute autochthonous species of their own; thus they have relatively numerous species. Those remote from sources of immigrants have, as previously noted, fewer species, and often a higher proportion of autochthonous ones. Groups of narrowly separated islands may collectively have a reinforcing effect on one another's biotas, and may act as evolutionary centres somewhat as the continents do. Similar relationships seem

to obtain for marine and to a lesser extent for fresh-water habitats, though so far as I know they have not been so explicitly worked out, and they are modified in some respects by the very different conditions of life.

One of the consequences of this geographic pattern is that in large, rich habitats the rate of progressive evolution, because of both the high rate of speciation and the large number of species competing and undergoing selective improvement at any one time, should be higher than in remote and restricted habitats. It is true that these latter sometimes act as subsidiary centres of evolution, but the results in terms of effective level of adaptation must be expected to be inferior to those of continental habitats, where both the variety of species serving as raw materials to the evolutionary process and the competitive drive that acts to shape them are so much greater. That such differentials of adaptive level indeed exist is borne out by experience of introducing continental organisms into insular habitats and vice versa. Though insular forms have sometimes adapted themselves well to continental environments, and even become aggressive components of continental ecosystems, such examples are completely overshadowed by the widespread disruption that has been caused in island ecosystems by the introduction of continental organisms. It is likely that there are differentials among continents and among different islands also, but the whole subject requires controlled and quantitative study to supplement the excellent qualitiative accounts that now exist.

Systems Extended in Time

The ecological processes that we now see operating have of course gone on since a very early stage in the development of life. It is agreed that the general trend of evolution has been one of progressive adaptation, though this may perhaps have been only an overall trend, rather than a uniform movement. Particular phyletic lines have certainly undergone many vicissitudes; indeed, by mathematical necessity, the majority of them have become extinct. On the other hand, expansion of one line after another into dominance, often at the expense of some previously well established competitor, is a matter of geological record. Such expansion of a line often appears to be rather sudden, certainly the major segregates often are established very early in the evolutionary history, with both progressive evolution and proliferation into many species merely elaborating the initial framework.

One hypothesis advanced to explain the rise of groups to a position of relative dominance is that they have made some kind of a breakthrough, permitting them to use a larger share of the resources of their environment. Such breakthroughs may be of two different kinds. They may be *inventive*, involving the use of some previously unexploited habitat or resource. The colonization of the land by aquatic organisms was a major breakthrough of this type, whereas introduction of a new step into a food chain would be a minor one. Alternatively, breakthroughs may be *competitive*, depending on getting a share of resources that previously went to some other species or group. The first type of breakthrough results in an increase in the total productivity of the system. The second type involves no change in the total productivity, but only a change in its partition.

This hypothesis agrees well with the relationship among effective living space, richness in species, and level of progressive evolution postulated above for existing biotas. Stocks achieving a breakthrough, whether inventive or competitive, can by definition support far larger populations than before. They have in fact increased their effective living space, both absolutely and relatively. This would be expected in due course to increase their differentiation and the rate of their progressive evolution just as effectively as would an increase in the area inhabited or in its absolute productivity. Conversely, if another group of organisms, numerous and varied in species, suffers a sharp reduction in numbers of individuals as a result of expansion of the first, then it must be expected on a purely statistical basis to lose many of its species by extinction.

We do not know much about the history of the aggregate productivity of ecosystems. Obviously there has been an increase since the early days of simple primordial organisms. Obviously also there must have been increases with such major steps as the colonization of freshwater and terrestrial habits. Smaller inventive breakthroughs must have taken place many times, and are perhaps still taking place. An intelligent guess might therefore be that the overall trend of biotic productivity in comparable environments is upward, though perhaps not very dramatically so nowadays.

Certainly there must at times have been dramatic reversals of the trend. The Pleistocene glaciations, for example, denied large parts of the polar and north temperate zones to most forms of life. The space available for organisms in the North American continent was for instance greatly compressed, and there must have been serious decrease in average population numbers with consequent statistical increase in extinction rates. Every major change of world climate or of land and sea distribution must have caused similar disturbances in one habitat or another. We may therefore think of a seesaw progress, with the overall levels of both productivity and diversity of biota in general increasing but probably at a diminishing rate.

THE UNITY OF POPULATION BIOLOGY

The foregoing discussion only hints at the complexity of many of the processes and relationships here outlined in very elementary form. Some of the ideas presented are highly speculative and some will no doubt prove to be wrong. However, I hope enough has been said to establish what is really my main thesis: that there is underlying unity in the sciences that deal with living populations. Whether, as in systematics, we are studying the properties, mating systems and evolution of kinds of organisms; whether, as in genetics, we are studying the variation and heredity of these properties and kinds; or whether, as in ecology, we are studying the interaction of the kinds and their properties in a unified system, we are studying different aspects of the same general problem: the nature of populations, and of their short-term and long-term interactions with one another and the environment.

In the last generation we saw the union of systematics and genetics to form a general domain of descriptive and evolutionary population biology.

In the present generation we are seeing the union of systematics and genetics with ecology to form a general biology of populations and ecosystems. Dare we hope that in the next generation population biology will unite with the disciplines that deal with the internal processes of the organism, now themselves uniting as molecular biology? If this can be achieved—and the points of potential contact are many—we shall at last have laid the groundwork of a truly unified structure of biological theory.

REFERENCES

ARRHENIUS, O. 1921
    Species and area. *J. Ecol.* 9: 95–99.
BROWN, W. L., JR., AND E. O. WILSON. 1956
    Character displacement. *Syst. Zool.* 5: 49–64.
FISHER, R. A., A. S. CORBET AND C. B. WILLIAMS. 1943
    The relation between the number of species and the number of in-
    dividuals in a random sample from an animal population. *J. Anim.
    Ecol.* 12: 42–58.
HAIRSTON, N. G. 1959
    Species abundance and community organization. *Ecology* 40: 403–
    416.
MACARTHUR, R. 1960
    On the relative abundance of species. *Amer. Nat.* 94: 25–36.
MUNROE, E. G. 1950
    The systematics of *Calisto* (Lepidoptera: Satyrinae), with remarks
    on the evolutionary and zoogeographic significance of the genus.
    J. New York Ent. Soc. 58: 211–240.
MUNROE, E. G. 1953
    The size of island faunas. *Proc. Seventh Pacific Science Congr.* 4:
    52–53.
MUNROE, E. G. 1958 .
    Systematics as a tool in ecology. *Proc. Tenth Intern. Congr. Ent.* 2:
    663–667.
MUNROE, E. G. 1963
    Perspectives in biogeography. *Can. Ent.* 95: 299–308.
PRESTON, F. W. 1948
    The commonness, and rarity, of species. *Ecology* 29: 254–283.
PRESTON, F. W. 1962
    The canonical distribution of commonness and rarity. *Ecology* 43:
    185–215, 410–432.
WILLIAMS, C. B. 1944
    Some applications of the logarithmic series and the index of diversity
    to ecological problems. *J. Ecol.* 32: 1–44.
WILLIAMS, C. B. 1947
    The logarithmic series and the comparison of island floras. *Proc.
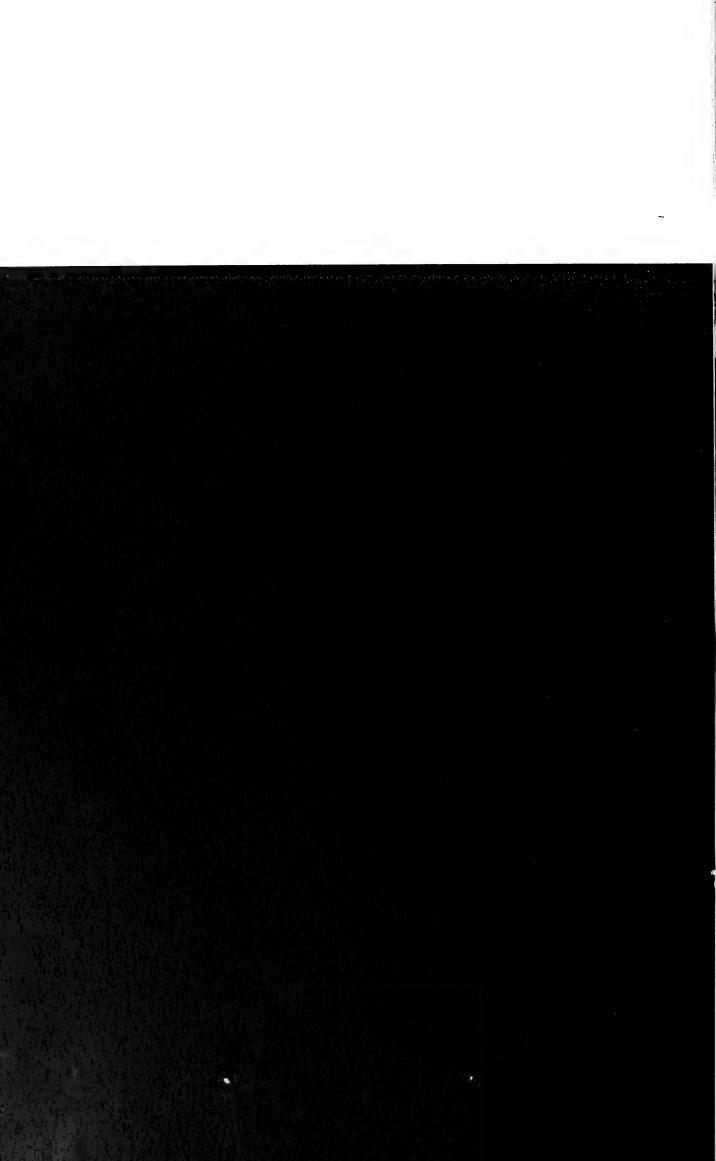   Linn. Soc. London* 158: 104–108.
WILSON, E. O. 1959
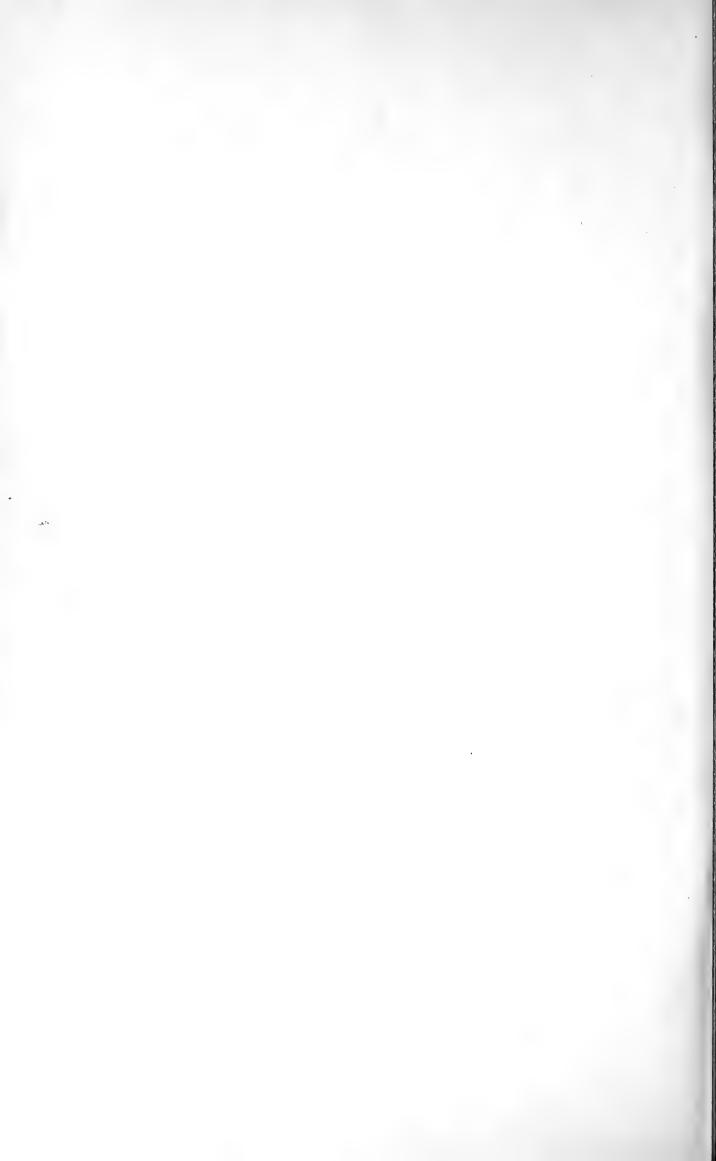   Adaptive shift and dispersal in a tropical ant fauna. *Evolution* 13:
    122–144.